

Ontogeny of Body Size Variation in African Apes

STEVEN R. LEIGH AND BRIAN T. SHEA

Department of Anthropology, University of Illinois, Urbana, Illinois
61801-3672 (S.R.L.), Departments of CMS Biology and Anthropology,
Northwestern University Medical School, Chicago (B.T.S.),
Illinois 60611-3008

KEY WORDS Primates, Growth and development, Growth spurt

ABSTRACT Size variation in African apes (*Gorilla gorilla* [gorilla], *Pan paniscus* [pygmy chimpanzee], and *Pan troglodytes* ["common" chimpanzee]) is substantial, both within and between species. We investigate the possible evolutionary significance of this variation through an analysis of the ontogeny of size variation in this group. In addition, we highlight possible areas of future endocrinological research, and evaluate recently proposed alternative models that attempt to account for ontogenetic variation in apes. The present study shows that intergeneric variation in size is largely a consequence of differences among species in the rate of body weight growth. Interspecific size variation in *Pan* is a product of both rate and duration differences in growth. The ontogenetic bases of sexual dimorphism vary in this group. Dimorphism is largely a result of sex differences in the duration of body weight growth in gorillas and pygmy chimpanzees, but results from differences in the rate of growth in common chimpanzees. Ontogenetic analyses largely confirm earlier interpretations, but with better data and methods. The great degree of ontogenetic variation within and among these species, especially in the timing and magnitude of "pubertal" growth spurts, implies that studies of endocrine growth control in African apes could be a productive line of future research. We also suggest that ontogenetic variation can be understood with respect to ecological risks. Growth rates seem to be negatively correlated with ecological risk in African apes, suggesting links between ontogenetic patterns and social and ecological variables. High growth rates in gorillas compared to *Pan* are most consistent with this model. Variation between chimpanzees and pygmy chimpanzees (especially females) also seem to fit predictions of this model. © 1996 Wiley-Liss, Inc.

Adult size variation within and among African ape species (*Gorilla gorilla* [gorilla], *Pan paniscus* [pygmy chimpanzee], and *Pan troglodytes* ["common" chimpanzee]) is relatively well documented (Harvey et al., 1986; Fleagle, 1988; Jungers and Susman, 1984; Shea, 1983; Uehara and Nishida, 1987). This information is critical to understanding nearly all aspects of ape biology and has significant implications for a broad range of research questions (Calder, 1984; Doran, 1993; Fleagle, 1985; Jungers, 1985; Schmidt-Nielsen, 1984). Despite fairly good documen-

tation of adult size variation in African apes, there is uncertainty about the exact nature and evolutionary significance of this variation within and among these species (cf. Doran, 1993). More importantly, reliable data about the ontogenetic bases of adult size variation in these species are rare, pre-

Received February 22, 1994; accepted September 28, 1994.

Address reprint requests to Steven R. Leigh, Department of Anthropology, University of Illinois, 109 Davenport Hall, 607 S. Mathews St, Urbana, IL 61801-3672.

cluding detailed assessments of the significance of sexual and specific size differences in this group.

Information about ontogeny is central to the interpretation of adult size variation because ontogenies are subject to evolutionary pressures (e.g., natural and sexual selection) (see Gould, 1977; Shea, 1983, 1990, 1992). In addition, ontogenetic differences within and among species may be related to alternative evolutionary forces that are not necessarily strongly correlated with terminal adult size (DeRousseau, 1990; Shea, 1990). This problem is clearly illustrated in studies of sexual size dimorphism in which similar levels of adult body size dimorphism can be shown to have variable ontogenetic bases (Leigh, 1992a,b; Shea, 1986). An ontogenetic perspective provides insight into the evolutionary significance of size variation by allowing direct investigation of key life history variables that ultimately control adult size, including growth rates (Janson and van Schaik, 1993) and ages at maturation (Stearns, 1992). Thus, the present analysis attempts to link information about size ontogeny to hypotheses about life history variation in apes. Our basic objectives are to evaluate and extend Shea's (1983) proposal that two distinct processes result in adult size differences within and among ape species. His comparisons indicated that sex differences in the duration of growth were mainly responsible for sexual size dimorphism within species. On the other hand, differences in rates of growth seemed to account for variation in adult size among species. These results suggested that the allometric extensions within and among African ape species could be accounted for by differing heterochronic processes. Furthermore, Shea suggested that differences in growth rates and durations that influenced heterochronic processes could be linked to sexual selection (intraspecifically) and to ecological differences (interspecifically).

Shea's absolute growth data were quite variable in terms of sample size and quality, limiting his conclusions to rather general statements. The comparatively low quality of absolute growth data available at that time obviously precluded insight into more subtle aspects of ontogeny (e.g., variation in

growth spurts), which have significant consequences for adult size and may be associated with important evolutionary variables (Leigh, 1992a,b, 1994a,b). In addition, a much better understanding of African ape socioecology (Wrangham, 1986) and life history strategies (Watts and Pusey, 1993) has become available since Shea's (1983) analysis. These new data create an opportunity for more detailed knowledge of the ontogenetic processes that result in terminal adult size in these species. Finally, powerful analytical methods for the analysis of ontogenetic data have been developed in the last decade.

Information about variation in ontogeny serves as a foundation for extension of Shea's previous research into two major areas. First, an understanding of variation in body weight ontogeny is a necessary initial step for investigations of the endocrine control of growth in apes, particularly since other measures of size growth (e.g., trunk length) from individuals of known age are very rare. We explicitly intend our analyses to provide information that could be relevant to endocrinological analyses of these species. Second, hypotheses about evolutionary factors that influence adult size can be presented. We develop these hypotheses within a theoretical framework that makes predictions about the adaptive significance of ontogenetic variation in primates. Specifically, we present a preliminary evaluation of Janson and van Schaik's (1993) hypothesis that growth at a slow rate is a risk aversion strategy in social primates. This life history strategy evolves as a consequence of ecological risks that result primarily from intraspecific feeding competition. Growth at a slow rate is a feasible response to feeding competition because it minimizes chances of death per unit time by reducing metabolic costs of growth. This ontogenetic "option" is available to primates because group life is thought to moderate predator pressure, which otherwise favors rapid maturation. Evaluation of Janson and van Schaik's (1993) hypothesis is especially important for apes because a previous analysis (Watts and Pusey, 1993) raises important questions about the ability of this model to adequately explain ontogenetic variation in apes. There-

TABLE 1. Comparative developmental information for African apes

Variable	<i>Gorilla gorilla</i>	<i>Pan paniscus</i>	<i>Pan troglodytes</i>
Sample size	72 F, 64 M	13F, 23M	22 F, 23 M
Average birthweight	2,327 g	1,467 g	1,766 g
Average gestation length ¹	259 days	228 days	232 days
Average prenatal growth rate	8.98 g/day	6.43 g/day	7.61 g/day
Mean captive adult weight (g)			
Male	169,000	46,870	57,150
Female	80,250	33,940	45,000
Literature-reported Adult Weight (g) ²			
Male	169,500	45,000	60,000
Female	71,500	33,200	47,400
Weaning age ³	3–4	—	5
First labial swelling	8	ca. 7	6–7
First adult-sized sexual swelling	—	—	10
Age at menarche	7–8	ca. 9	11
Female first birth	10–12	ca. 13–15	14–15
Start testes growth accel.	—	ca. 9	9
First ejaculation	ca. 9	—	9
Adult-sized scrotum	ca. 9	—	12–13

¹ Ardito (1976)² Jungers and Susman (1984).³ These and all subsequent data from Watts and Pusey (1993) and expressed in years.

fore, we present a preliminary evaluation of this hypothesis with absolute growth data from African apes.

MATERIALS AND METHODS

Materials

Chronological age and weight measures were derived from 222 captive African apes housed at zoological parks and primate centers throughout the world (Table 1). All weight measures were derived from clinically normal animals, and additional information about this sample is detailed elsewhere (Leigh, 1992a,b, 1994a,b; Leigh and Shea, 1995). With the exception of a small number of individuals (10 gorillas older than 19 years of age and 5 pygmy chimpanzees older than 13 years of age) all ages are exact to the day. Both absolute (weight for age) and specific growth are investigated. Specific growth rates are measured by dividing growth rate at each age by predicted size at that age. These estimates can be used in appraising differences in growth rates independent of size.

Analyses of subspecies are not undertaken. Gorillas are represented solely by the western lowland subspecies (*Gorilla gorilla gorilla*). Pygmy chimpanzees are not currently allocated to different subspecies. The "common" chimpanzees in this sample are of unknown subspecies. Subspecific variation

(Groves, 1970; Morin et al., 1994; Shea et al., 1993) in ontogeny could be important for these species, but data for various subspecies are not available. In addition, ontogenetic data from wild animals are currently unobtainable. Thus, data from captive animals supply information about ontogeny in these species. We assume that captivity does not radically alter the general pattern of interspecific differences in ontogeny, although precise rates and durations of growth may differ from wild populations. It can be noted that correlations between captive and wild-shot weights are high (Leigh, 1994b) and that the relevance of captive data to evolutionary problems has been discussed previously (Leigh, 1992a,b, 1994a,b).

Estimates of gestation length are obtained from literature sources (Ardito, 1976; Harvey et al., 1986). Gestation lengths for each species are averaged from multiple values given by Ardito, and are used to calculate total age (age from conception) and mean prenatal growth rates.

Methods

Data treatment. All mixed-longitudinal data are treated cross-sectionally in this study. This procedure precludes analyses of individual variation in ontogeny, but does provide information that is adequate for comparisons of growth among groups (spe-

cies or sexes within a species) (Eveleth and Tanner, 1990; Tanner, 1978). Description of cross-sectional growth can be shown to give an approximation of the average of growth trajectories based on longitudinal treatment of the data (Leigh, 1992a; Dielman, 1989), and can thus be considered appropriate for group comparisons.

Nonparametric regression. Nonparametric lowess and loess regressions (Cleveland, 1979; Cleveland and Devlin, 1988; Efron and Tibshirani, 1991) are employed to provide an empirical description of growth for each sex in each species. These methods are extremely flexible, and are optimal in interspecific comparisons of ontogeny because the resulting descriptions of growth are not dependent on the functional form of a particular regression model. Both forms of regression iteratively fit a line through segments of a bivariate distribution in a number of steps (Efron and Tibshirani, 1991).

Lowess smoothing robustly fits a scatterplot because residuals are inversely weighted (Cleveland, 1979). Lowess is used for basic description of ontogenetic trajectories. However, 95% bootstrapped confidence intervals are generated using loess (nonrobust) fits to the data with S-Plus statistical software (S-Plus, 1991). Programs that accomplish bootstraps with lowess fits are, to our knowledge, presently unavailable. In addition, confidence intervals from loess regression are more conservative than those based on lowess fits because residuals are not inversely weighted. Confidence intervals are presented for intraspecific plots and in selected interspecific comparisons. We should note that the structure of the data (unbalanced and longitudinal) greatly complicates traditional significance testing (see Dielman, 1989; Schneiderman, 1992).

Parametric regression. The "JPPS" parametric regression model, developed by Jolicouer et al. (1988, 1991), is used in this study to describe absolute growth in mass. Although originally developed to describe human statural growth, this model appears to describe weight growth in African apes well, and has been shown to model a wide range

of variation in human growth (including pathological cases [Pontier, et al., 1988]). The JPPS model, like others developed by Jolicouer and colleagues, relies on estimates of total age (=postnatal age plus length of gestation period). The main advantage of using total age is that the regression line passes through the origin ($X = 0, Y = 0$). Jolicouer (1985) suggests that this feature is desirable because it is biologically realistic to consider the size at fertilization (that of a single cell) negligible and nearly equal for all animals. Thus, a curve that passes through the origin is biologically more plausible with respect to somatic growth than are curves designed to describe population growth (as are most commonly encountered growth curves). The JPPS growth curve is given by the equation

$$Wt = A\{1 - 1/[1 + (Age/D1)^{C1} + (Age/D2)^{C2} + (Age/D3)^{C3}]\}.$$

Jolicouer et al. (1991, Table 1) describe D1, D2, and D3 as time scale factors (in years) and C1–C3 as dimensionless exponents. They find that the JPPS model fits human growth curves more adequately than Preece-Baines models because the JPPS model passes through the origin, and describes human growth at all ages equally well (unlike some kinds of Preece-Baines models).

Estimates of growth rates for both nonparametric and parametric regressions are calculated by dividing the difference in successive predicted weight values (Y) by the difference in successive age values (X) (equivalent to Coelho et al.'s [1984] pseudo-velocity curves). Pseudo-velocity curves yield approximations of the first derivative for each sex in each species and are useful in detecting the presence of growth "spurts." Although longitudinal data are ideal in the detection and calibration of growth spurts (Tanner, 1978), cross-sectional data can reveal their presence. It is possible that cross-sectional data consistently underestimate the magnitude of peak velocity, but this depends on the level of variation in individual growth within a group. In essence, cross-sectional data can be expected to provide conservative estimates of both the presence of a growth spurt and peak velocity if individ-

ual variance in growth is high. We are also investigating species in which growth durations are short compared to humans, limiting the degree of possible variance in the timing of growth spurts. Finally, specific growth rates are intended to evaluate size-independent rates of growth.

Interpretations of distance and pseudo-velocity curves are supplemented by comparisons of "size trajectories" among groups (e.g., among species by sex or within species between sexes). These curves compare sizes for each species or sex at equal ages and are bivariate plots of the JPPS model's predicted size values for each group at common ages. Size trajectories provide direct information about intersexual and interspecific ontogenetic size differences. In these plots, a line of identity ($Y = X$) represents completely shared ontogenetic trajectories. Deviations from this line indicate size differences at common ages that are a consequence of growth rate discrepancies (or differences in the duration of growth). In size trajectory plots, the case with the smallest adult size is plotted on the X axis, while larger cases are plotted on the Y axis.

Lowess regressions and several statistical tests are accomplished with either with Systat (Wilkinson, 1990) or StatXact (Mehta and Patel, 1992). StatXact uses exact permutational methods in statistical tests. Confidence intervals for loess regressions are calculated with S-Plus statistical software (S-Plus, 1991). All confidence intervals are calculated at the 95% level. Finally, a probability value of .05 is chosen as a critical value for estimates of statistical significance.

RESULTS

Birth weight and average prenatal growth rates

Birth weights among African apes vary in directions that are consistent with adult size (Table 1, Fig. 1). Gorilla neonates are, on average, the largest (2,327 g), followed by common chimpanzees (1,766 g), and pygmy chimpanzees (1,467 g). Samples for gorillas and pygmy chimpanzees are rather small. Exact permutational Kruskal-Wallis tests for gorillas and common chimpanzees suggest that there are no significant differences

in sexual size dimorphism at birth in these species ($P = .1905$ for gorillas; $P = .1183$ or $.7335$ for chimpanzees, depending upon whether or not an aberrantly small male value is used). Male gorillas tend to be consistently larger than females, a pattern not observed in the other species. The lowest birthweight of any animal is observed for a male common chimpanzee.¹ Differences in birthweight between gorillas and either *Pan* species (sexes combined) are statistically significant, as are differences between pygmy and common chimpanzees (Table 2).

Average prenatal growth rates, calculated by dividing average birthweight by average gestation length, vary among these species (Table 1). Gorillas grow at the highest average prenatal growth rate (8.98 g/day). The average prenatal growth rate in common chimpanzees is slightly slower (7.61 g/day), and the average pygmy chimpanzee growth rate is the slowest (6.43 g/day). Unfortunately, statistical tests on these values are not possible with the available data. However, some estimate of the range of variation is provided by dividing average birthweight by the extremes of reported gestation lengths (Table 3). Ranges suggests that gorillas and pygmy chimpanzees do not overlap in terms of average prenatal growth rate. On the other hand, common chimpanzee growth rates could overlap with the other African apes. Maximum possible ranges (lowest birthweight divided by longest reported gestation and highest birthweight divided by shortest reported gestation) overlap to a great degree among these species.

Post-natal growth

Comparisons among species

Gorilla vs. *Pan*. Estimates of growth curves based on parametric and nonparametric models are consistent in their measurement of growth differences among species (Figs. 2, 3; see Table 4 for parameter

¹It should be noted that this very small male survived birth and was alive for its most recent weight at the age of 4 years. All early postnatal weights for this animal are very low, implying that measurement error is not responsible for the low birthweight. Our records are not sufficient to determine if this animal was premature or if there were clinical complications to the pregnancy.

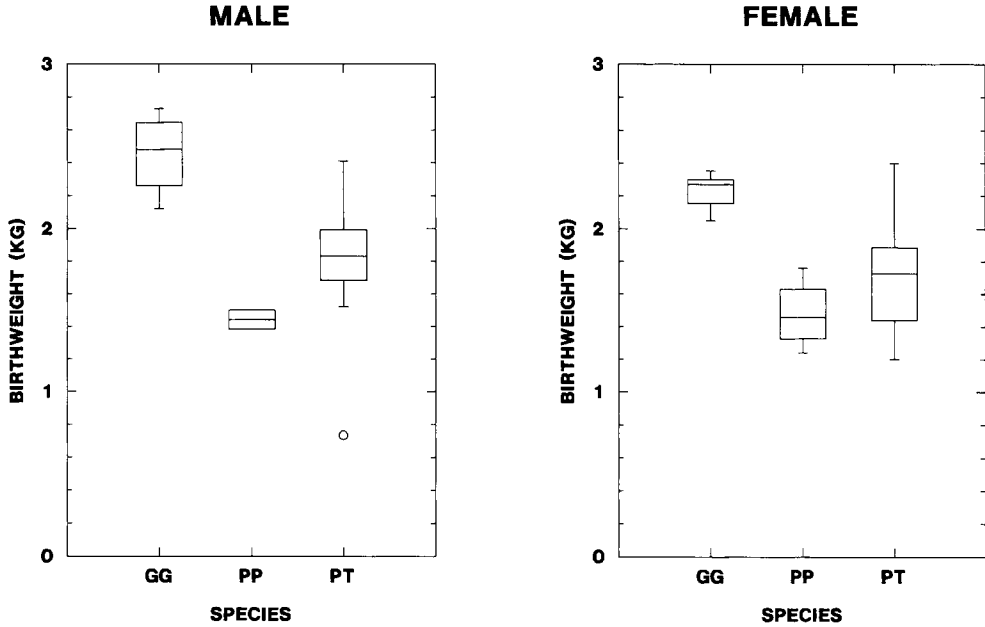


Fig. 1. Box and whiskers plots of birthweights for male and female African apes. In this and in subsequent plots, "GG" refers to *Gorilla gorilla*, "PP" refers to *Pan paniscus*, and "PT" to *Pan troglodytes*.

TABLE 2. Exact permutational tests for significant differences in birthweight among species (sexes are combined)

<i>Gorilla gorilla</i> vs. <i>Pan paniscus</i>	0.0004
<i>Gorilla gorilla</i> vs. <i>Pan troglodytes</i>	0.0000
<i>Pan paniscus</i> vs. <i>Pan troglodytes</i>	0.0150
<i>Gorilla gorilla</i> vs. <i>Pan troglodytes</i> (excludes unusually low value)	0.0000
<i>Pan paniscus</i> vs. <i>Pan troglodytes</i> (excludes unusually low value)	0.0074

TABLE 3. Estimated minimum and maximum average prenatal growth rates for African apes¹

	<i>Gorilla gorilla</i>	<i>Pan paniscus</i>	<i>Pan troglodytes</i>
Minimum	8.05	5.64	6.54
Maximum	9.27	7.48	8.41

¹ Values are calculated by dividing the average birthweight by minimum and maximum reported gestation lengths [Ardito, 1976]. All values in g/day.

values; bivariate data plots of age and mass data and confidence intervals are presented along with intraspecific comparisons). Gorillas can be expected to grow faster than either pygmy chimpanzees or common chimpanzees during postnatal growth, continuing a prenatal trend. Growth durations vary such

that female gorillas cease growth earlier than female common chimpanzees but later than female pygmy chimpanzees. On the other hand, male gorillas cease growth later than *Pan* males. Curves of specific growth rates plotted against age suggest that female gorillas generally exhibit relatively higher growth rates than either *Pan paniscus* or *Pan troglodytes*, with the most pronounced differences early in ontogeny (Fig. 4). Specific growth rates for male gorillas are also generally higher than specific growth rates for *Pan*.

Size trajectory curves confirm results based on inspection of distance and pseudo-velocity curves. Curves for males suggest that gorillas do not overlap in size with either chimpanzees or pygmy chimpanzees (Figs. 5, 6). Comparisons of size trajectories for females present a similar situation. Thus, female gorillas do not, on average, share size trajectories with either of the other two species.

***Pan paniscus* vs. *Pan troglodytes*.** Size differences between the *Pan* species are related to both rate and duration of growth.

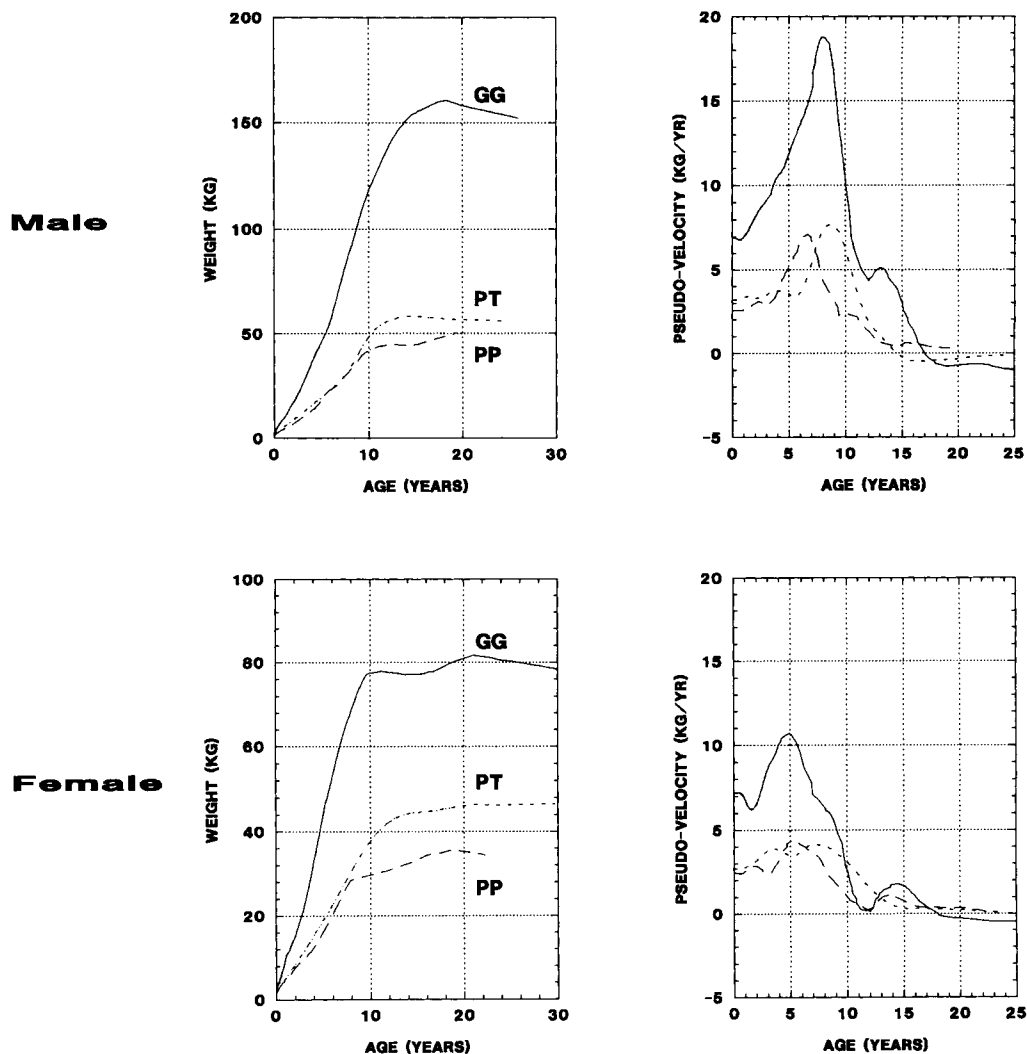


Fig. 2. Lowess-estimated (robust locally weighted least squares) growth curves for African apes by sex. The left-hand column contains distance (estimated weight for postnatal age), and the right-hand column presents pseudo-velocity curves (kg/year by age). Individual weight and age observations are presented in plots for intraspecific analyses. "GG" refers to *Gorilla gorilla* (solid line), "PT" to *Pan troglodytes* (dotted line), and "PP" to *Pan paniscus* (dashed line).

Early postnatal growth rates are quite comparable between these species for both sexes (Figs. 2, 3). However, both parametric and nonparametric regressions suggest that growth rates and durations vary between sexes and species. Male growth in *Pan paniscus* proceeds at a slower rate than *Pan troglodytes* between the ages of one and four years, but a clear male *P. paniscus* growth spurt eliminates any average size difference

between 6 and 8 years. On the other hand, female pygmy chimps are, on average, consistently smaller than female common chimps, despite higher growth rates between 4 and 6 years of age. Growth rates in *Pan paniscus* are more varied than *Pan troglodytes* prior to 8 years of age. Adult female common chimpanzees are larger than adult pygmy chimpanzees mainly because they have higher growth rates very early and

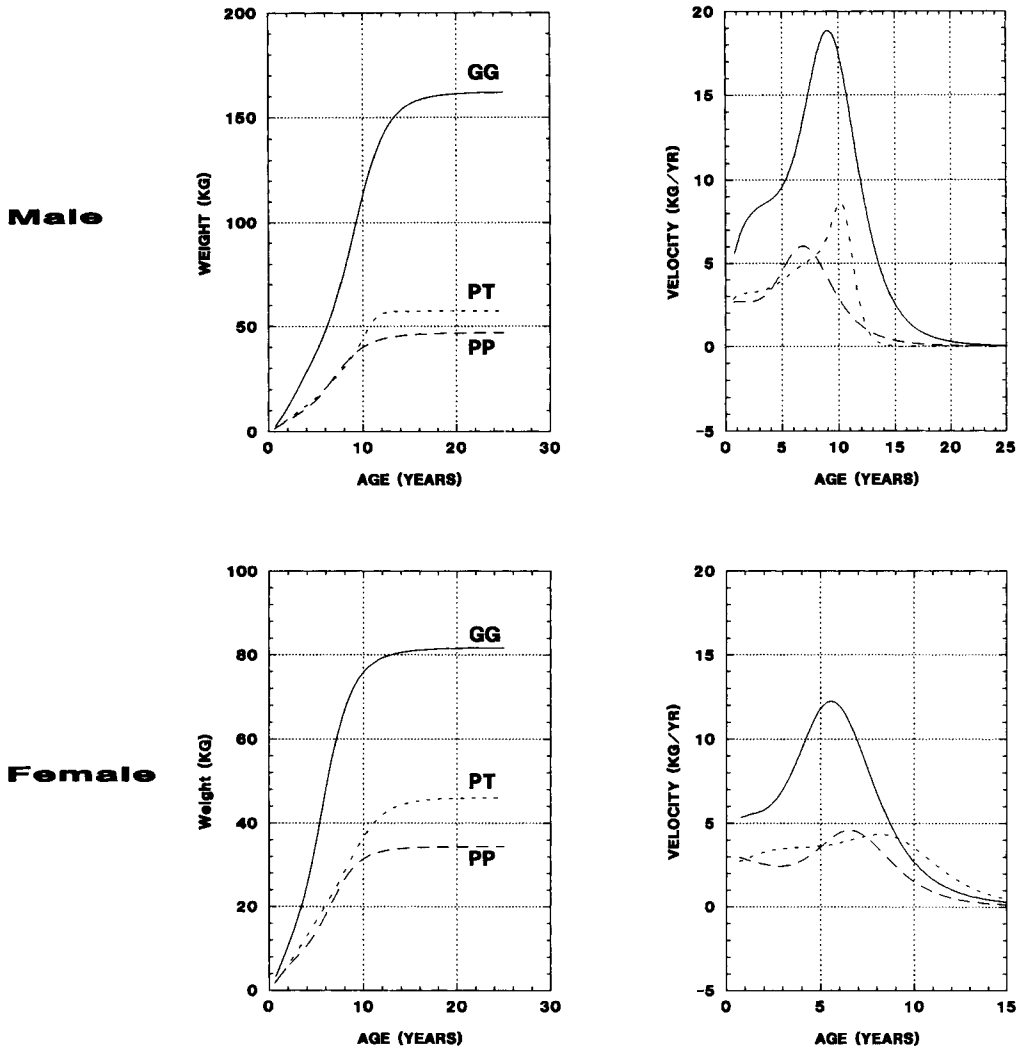


Fig. 3. Parametric growth curves (JPPS model) for African ape species.

grow for a much longer period of time. In females, more rapid later growth in pygmy chimpanzees does not, on average, compensate for slower early growth. Confidence intervals on slopes comparing female growth in *Pan* (Fig. 7) indicate that the predicted size trajectory for common chimpanzees is at the extreme upper confidence interval for pygmy chimpanzees at around three years of age. However, upper and lower confidence intervals for pygmy chimpanzees exceed their counterparts for common chimpanzees by about 7 years of age. Finally, plots of spe-

cific growth rates show that the relation between these two species size-adjusted growth rates vary through time in a manner similar to absolute growth trajectories (Fig. 4).

Analyses of covariance suggest the presence of statistically significant differences for females (Table 5). For females (assuming a linear growth rate, and independence among observations), the average growth rate for *Pan troglodytes* between the ages of one and six years of age significantly exceeds the average growth rate for *Pan paniscus*. The difference is not statistically significant

TABLE 4. Parameter estimates and standard errors for parameters from the JPPS model

Case	A	D1	C1	D2	C2	D3	C3
Male <i>Gorilla</i>	162	9.44	6.94	11.85	1.44	16.21	6.94
SE	1.68	7.73	0.93	10.75	0.10	562.67	27.03
Female <i>Gorilla</i>	81.79	8.73	5.51	10.40	1.18	6.33	4.94
SE	1.06	132.30	4.24	1.78	0.17	15.80	1.13
Male <i>P. paniscus</i> (SEs not computable)	47.01	39.02	5.24	7.39	5.30	12.89	1.12
Female <i>P. paniscus</i> (SEs not computable)	34.42	35.09	5.90	6.85	5.90	9.28	1.07
Male <i>P. troglodytes</i>	57.33	9.19	4.79	9.97	19.03	12.12	1.22
SE	0.51	0.53	2.50	0.40	6.24	5.39	0.29
Female <i>P. troglodytes</i>	46.04	8.48	1.92	8.93	6.95	44.81	0.79
SE	0.69	8.30	3.32	1.05	2.51	747.54	2.76

between the ages of 2 and 6 years, and a higher growth rate is observed in *Pan paniscus*. Male growth rates during these intervals are not significantly different.

Size trajectories clearly illustrate interspecific contrasts in absolute growth. Males follow a very similar ontogenetic trajectory almost until pygmy chimpanzees reach adult size (Fig. 5). However, females can be expected to share common sizes at common ages only for the earliest part of ontogeny (Fig. 5). Female size trajectories show that female common chimpanzees are consistently larger than pygmy chimpanzees, even though growth rates in *Pan paniscus* are higher later in ontogeny.

Comparisons within species

Gorilla. The African ape species all attain at least moderate levels of sexual size dimorphism (Jungers and Susman, 1984; Leigh and Shea, 1995; Shea, 1985, 1986). Nonparametric lowess regressions suggest that male and female gorilla growth curves diverge at approximately 6–7 postnatal years (Fig. 8). Female growth then ceases at approximately 9.5–10 years of age. Males continue growth beyond this age. Pseudo-velocity curves for gorillas suggest that female and male growth rates are stable for the first year. After this point, the male growth rate increases, while the female growth rate decreases. The female growth rate then increases, attaining a cross-sectionally defined peak velocity of about 11 kg/year at 5 years of age. The growth rate then declines steadily. Male peak velocity is attained at approximately 8 years of age at slightly under 19 kg/year, then declines.

Fluctuation of growth rates at older ages is a consequence of variation in sample size. Specific growth rates are very similar, and differences in the shapes of the curves are most obvious at the peak of the male growth spurt (Fig. 9).

Parametric curves modeled by the JPPS curve suggest a pattern consistent with other methods (Fig. 10). However, these curves indicate minimal average divergence until around eight years of age, and the female growth period appears to be slightly longer when growth is described in this manner. Pseudo-velocity curves indicate very high early growth rate in male gorillas, suggesting the initiation of a "pubertal" growth spurt at about five years of age. Peak velocity measured by the JPPS curve for males is comparable to peak velocity measured through lowess regression. However, the JPPS curve shows that the velocity peak is later than suggested by lowess regression for both females and males. Parametric curves imply that average female growth rate exceeds the male growth rate between 4 and 6 years of age. This contrasts with the nonparametric model which suggests that, on average, female growth rates after 1 year of age can be expected to be lower than male growth rates.

The intraspecific size trajectory for *Gorilla* is nonlinear (Fig. 11), indicating fluctuations in growth rate differences between sexes. Substantial differences in size trajectories arise as both sexes approach the 60 kg size range.

Pan paniscus. Pygmy chimpanzees exhibit a pattern of dimorphic ontogeny that is similar to *Gorilla* in its general features

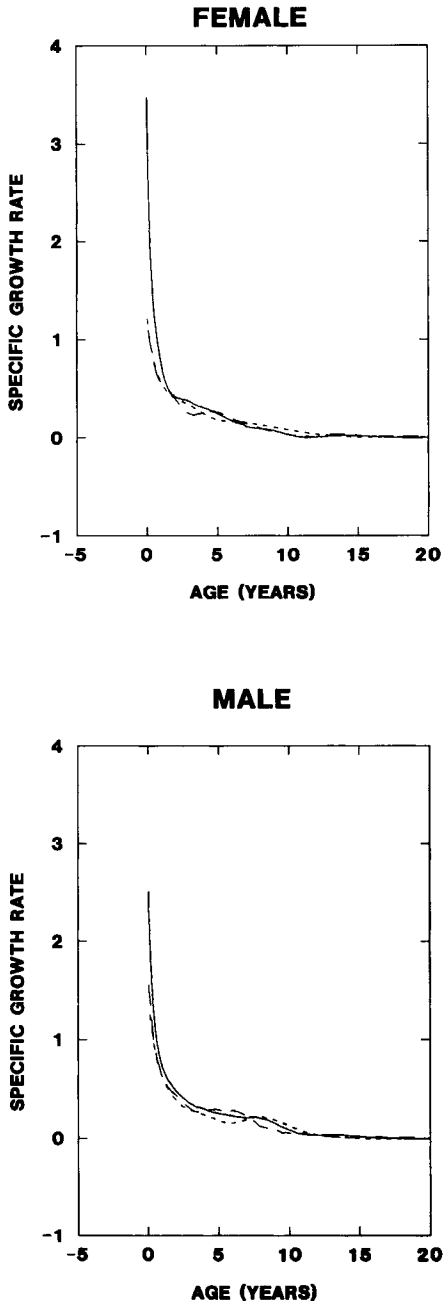


Fig. 4. Specific growth rates for African apes by sex. The solid line shows specific growth rates for *Gorilla gorilla*, the dotted line is for *Pan troglodytes*, and the dashed line represents *Pan paniscus*. The specific growth rate is calculated by dividing the rate of growth at time t by predicted mass at time t .

(Fig. 8). Male and female curves diverge slightly at around five years of age (although this may be a sample-dependent observation). Females appear to cease growth prior to 10 years of age, whereas males continue to grow until approximately 11–12 years of age. Pseudo-velocity curves indicate the possible presence of “mid-” and “pubertal” growth spurts in females and males (Tanner, 1978), although more adequate longitudinal data are clearly needed in precisely measuring these attributes. Both sexes apparently initiate these spurts at about the same age. Average peak velocity for female pygmy chimpanzees is about 4.25 kg/year just after five years of age. Males attain a peak velocity of about 7 kg/year at about seven years of age. Both absolute and specific growth rates vary the most at the age of peak velocity (Fig. 9).

Parametric curves are comparable to non-parametric curves for this species (Fig. 10). However, parametric pseudo-velocity curves suggest a consistent diminution of growth rates prior to the initiation of a “pubertal” growth spurt. Moreover, parametric models reflect smaller sex differences in the timing of growth spurts than nonparametric measures. The male growth spurt is also less distinct in the parametric estimate than in the nonparametric estimate, possibly implying that nonparametric methods are more robust than some parametric models against problems of growth spurt estimation. In any case, sexual size dimorphism is related to sex differences in both rate and duration of growth in this species.

The intraspecific size trajectory plot suggests that males and females are comparably sized until they reach 10 kg (Fig. 11). After this point, males are larger than females. Size dimorphism increases slowly relative to gorillas.

***Pan troglodytes*.** Common chimpanzees differ from other African apes in the way that dimorphism is produced (Leigh and Shea, 1995). Both parametric and nonparametric distance curves suggest that males and females follow nearly identical ontogenetic trajectories until about 8 years of age (Figs. 8–10). Divergence of absolute and specific growth curves is observed at this age: the average growth rate in females appears

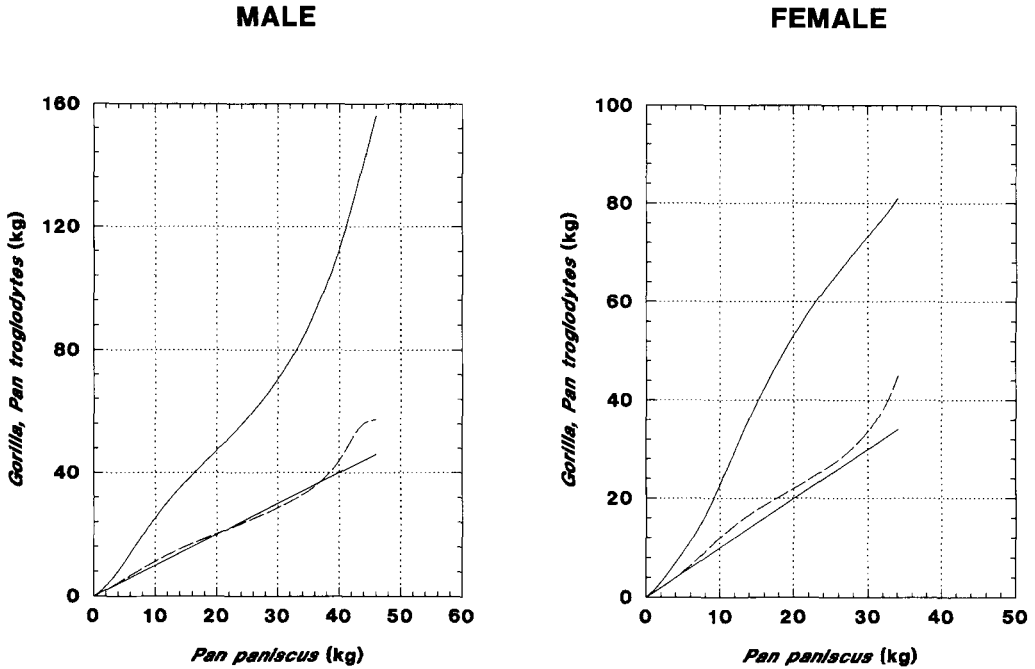


Fig. 5. Size trajectory curves for comparisons among species. These curves are obtained by plotting predicted size values at equal ages for each species. The solid straight lines represent identity ($y = x$). The uppermost solid lines are plots of predicted gorilla mass against predicted pygmy chimpanzee mass at equal ages. The

dashed lines represent plots of chimpanzee mass against pygmy chimpanzee mass. The solid line at $Y = X$ would represent values for pygmy chimpanzees plotted against themselves. These plots show the deviation in size among species at each point along a size trajectory for pygmy chimpanzees.

to be stable, but the average male growth rate increases. Pseudo-velocity curves suggest that males exhibit a pronounced pubertal growth spurt, but that females do not. Specifically, nonparametric curves for females indicate a slight increase and then fluctuation of average growth rate, with two possible and nearly equivalent peak velocities. Parametric pseudo-velocity curves are comparable, possibly suggesting that growth rates in females increase slowly until about 8 years of age. The apparently more prominent growth spurt in the parametric model is expected because the JPPS curve includes parameters that are intended to measure growth spurts, but these are difficult to specify because parameters are highly correlated. Both measures of ontogeny suggest that rate differences in growth account for the moderate level of dimorphism in this species (Leigh and Shea, 1995).

Size trajectory plots show that females

and males are similarly sized until about 22 kg (Fig. 11). After this point, size differences gradually arise, accelerating as the male growth spurt is initiated. Comparable ages at cessation of growth are reflected by the plateau at the upper end of the size trajectory.

DISCUSSION

This analysis facilitates emendment of previous analyses of the ontogeny of size differences within and between African ape species (Shea, 1983, 1985). First, Shea's (1983) general interpretations concerning absolute size growth within and between species were accurate, particularly for comparisons among species. We should stress that the present analysis does not explore heterochronic correlates of absolute size growth variation as did Shea (1983). However, our new data and methods reveal that

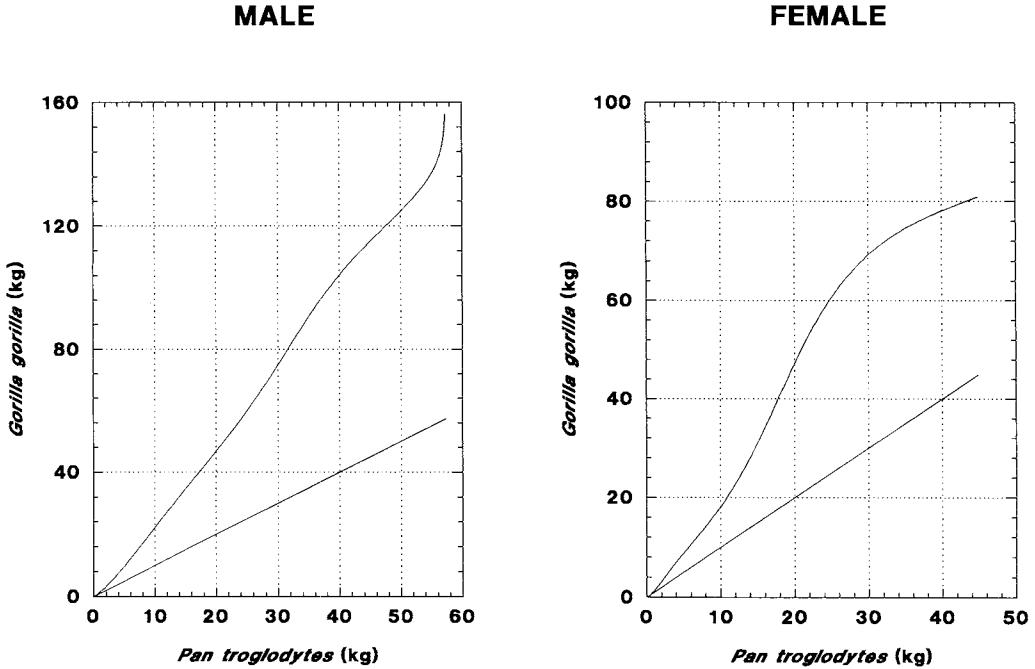


Fig. 6. Plot of gorilla mass against common chimpanzee mass at equal ages. The straight line represents identity ($y = x$).

adult size variation within and among species appears to involve greater variation in growth rates and durations than previously determined. Second, we can suggest that the present descriptions of mass growth have implications with respect to endocrine control of growth. Third, we can refine Shea's suggestion that sexual selection accounts for intraspecific size differences in apes while natural selection can account for interspecific size variation.

Ontogenetic processes

Differences in the rate of body weight growth are broadly responsible for the variation in adult size among these species, especially when gorillas are compared to either of the other two species. The effects of rate differences pervade ontogenetic comparisons: at no point during ontogeny (assuming linear prenatal growth trajectories) do either of the *Pan* species grow absolutely faster than gorillas. In addition, several maturation events occur earlier in gorillas (particularly females) than in *Pan* (especially com-

mon chimpanzees) (Table 1; Watts and Pusey, 1993).

Rate differences between gorillas and *Pan* are achieved through fluctuating growth rates. This is summarized most effectively by pseudo-velocity curves and by nonlinearity in size trajectory plots. Variation in the timing and magnitude of growth spurts appears to be particularly important in leading to size differences among these species. Although rate differences describe variation between *Gorilla* and *Pan* for both males and females, this general pattern is complicated by variation in growth duration. Specifically, a high growth rate in female gorillas relative to common chimpanzees is coupled with early maturation in female gorillas (Leigh and Shea, 1995; Shea, 1985, 1986; Watts and Pusey, 1993). This finding implies that factors responsible for the evolution of variation in both rate and time processes distinguish these species. The effects of differences in growth rate exceed the effects of differences in growth duration when female gorillas are compared to female common chimpanzees.

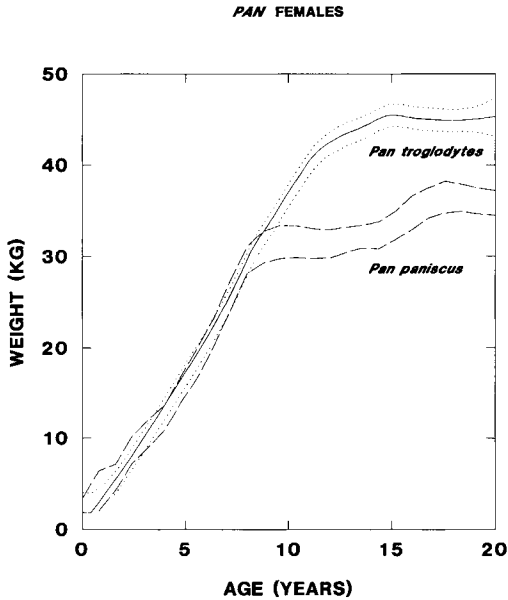


Fig. 7. Loess-estimated confidence intervals for pygmy and common chimpanzee females. The predicted slope for pygmy chimpanzees is not presented. The solid line represents the predicted slope for common chimpanzees, the dotted lines are upper and lower confidence intervals on the slope for common chimpanzees, and the dashed lines represent confidence intervals on the regression slope for female pygmy chimpanzees.

TABLE 5. Probability values for analyses of covariance for tests of significant differences in slope for selected age ranges in pygmy chimpanzees and common chimpanzees

Age (years)	Female	Male
1-6	.01	.21
2-6	.06	.10

On the other hand, only minimal differences in growth duration distinguish female gorillas from female pygmy chimpanzees. Comparisons among males suggest that rate differences mainly account for the size difference between gorillas and either of the two *Pan* species. However, extension of the male growth period in *Gorilla* contributes substantially to the final size differences between males of these genera. Thus, duration differences magnify intergeneric size differences among males that are initiated by growth rate differences. Contrasts in growth duration are largest when male gorillas are compared to male pygmy chimpanzees.

Differences in the duration of body weight growth are mainly responsible for size differences between *Pan troglodytes* and *Pan paniscus*. This pattern is especially obvious for males. Although common sizes are observed throughout much of ontogeny, differences in the timing of growth spurts are evident. Common sizes are maintained despite differences in underlying growth rates because an earlier growth spurt in male *Pan paniscus* allows this species to "catch-up" to common chimpanzees. This may imply that evolutionary forces have acted on different ontogenetic attributes or phases to yield animals of comparable size throughout the middle portion of ontogeny, and is consistent with the close similarities in allometric (Inouye, 1992; Shea, 1981, 1983, 1985) and behavioral (Doran, 1992) trajectories. Females do not share the striking similarities in distance curves and size trajectories at young ages that are apparent for males. Both absolute and specific growth rates in pygmy chimpanzee females do exceed those of common chimpanzee females for a substantial period of time, but size trajectories and distance curves show that pygmy chimpanzees do not exceed the size of common chimpanzees. It is possible that selection has resulted in greater differentiation among females than among males in *Pan*. Consequently, variation among females in the ontogeny of body size may be associated with important differences in female life history strategies (see below).

Sexual size dimorphism in African apes appears to have variable ontogenetic foundations. Modifications of Shea's (1983, 1985) assessments are required because data available in the early 1980s did not allow detailed specification of rate and time components of dimorphism. First, in each species, rate differences in body weight growth, including differences in the timing and magnitude of the growth spurt, influence adult dimorphism (Leigh, 1995; Shea, 1985, 1986). Second, differences in the duration of growth distinguish the sexes in each species, but gorillas and pygmy chimpanzees exhibit higher degrees of bimaturism than common chimpanzees. The sex differences in growth duration are lowest in common chimpanzees, leading to dimorphism that is produced

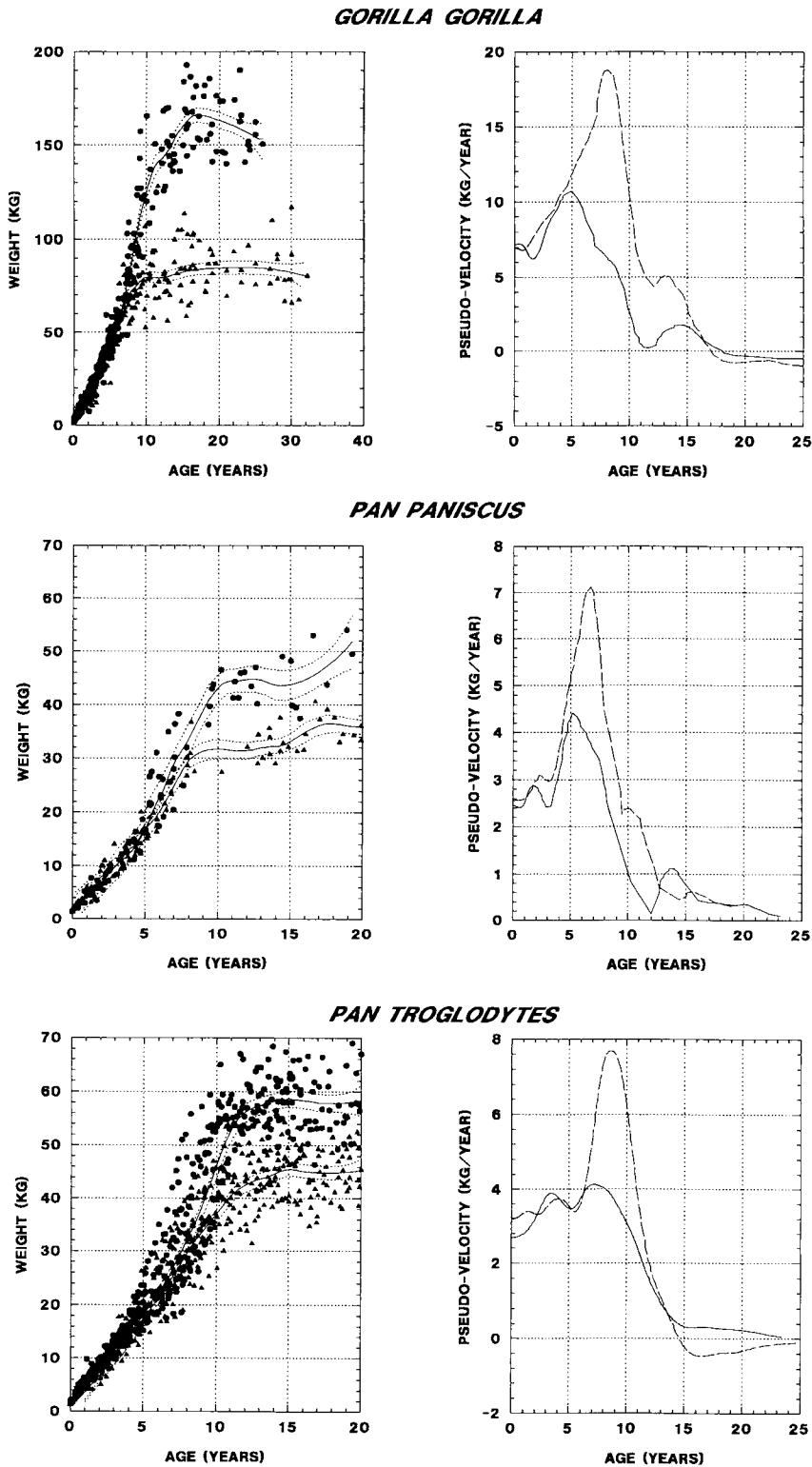
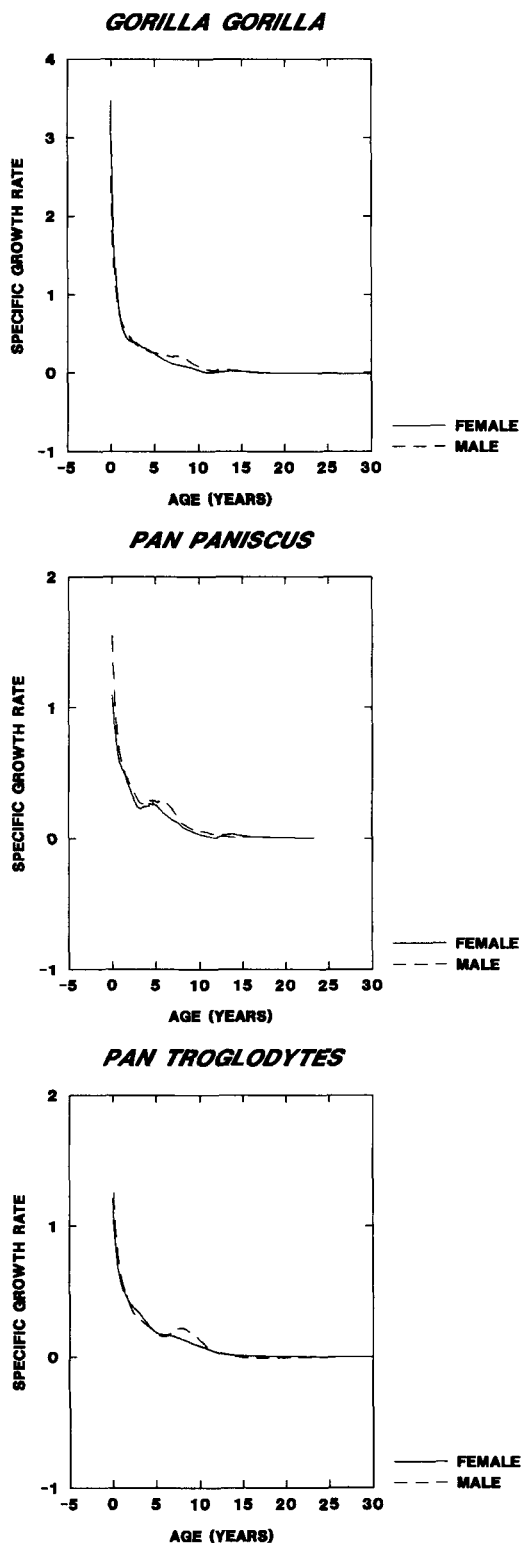


Fig. 8. Loess-estimated distance and pseudo-velocity curves for ontogenetic data by species. Males are represented by circles, females are shown by triangles for each species. In pseudo-velocity curves, females are depicted by solid lines, males by dashed lines.



largely through sex differences in the rate of growth (Leigh and Shea, 1995; Shea, 1985, 1986). The elevated level of bimaturism in *Pan paniscus* relative to *Pan troglodytes* results in a slight increase in sexual size dimorphism in the former species. Thus, the African apes become dimorphic in different ways; dimorphism in gorillas and pygmy chimpanzees is largely a consequence of differences in the duration of growth, and rate differences lead to sexual size dimorphism in common chimpanzees.

Endocrinological and evolutionary implications

This study clearly demonstrates that ontogenetic diversity in African apes is substantial. In view of this variation, we can articulate two major avenues of continuing research into analyses of ontogenetic and adult size variation within and among these species. First, it is apparent that this group of species offers an excellent opportunity to investigate the proximal (i.e., endocrine) determinants of variation in growth trajectories. Analyses of the hormonal bases of "pubertal" growth spurts in apes would seem to be an especially profitable line of research because the timing and magnitude of growth spurts vary within and between species. This variability implies that these very closely related species offer a good "natural experiment" for endocrinological research. Second, the present study evaluates the applicability of a hypothesis that predicts a negative correlation between growth rates and ecological risks in primates (Janson and van Schaik, 1993). Difficulties in the application of Janson and van Schaik's model to apes have recently been identified (Watts and Pusey, 1993), and the present analysis permits some resolution of these problems.

Endocrine growth control. Analyses of endocrine control in humans (Baumann et al., 1989; Merimee et al., 1987, 1991; Zachmann, 1992) may provide insight into ontogenetic variation in African apes. In humans, a multi-component cascade of biochemical events mediates the endocrine growth axis and associated receptor proteins, implying that comparable adult sizes can be produced through a variety of endocrine mechanisms (see review by Shea,

Fig. 9. Specific growth rates by sex for each species.

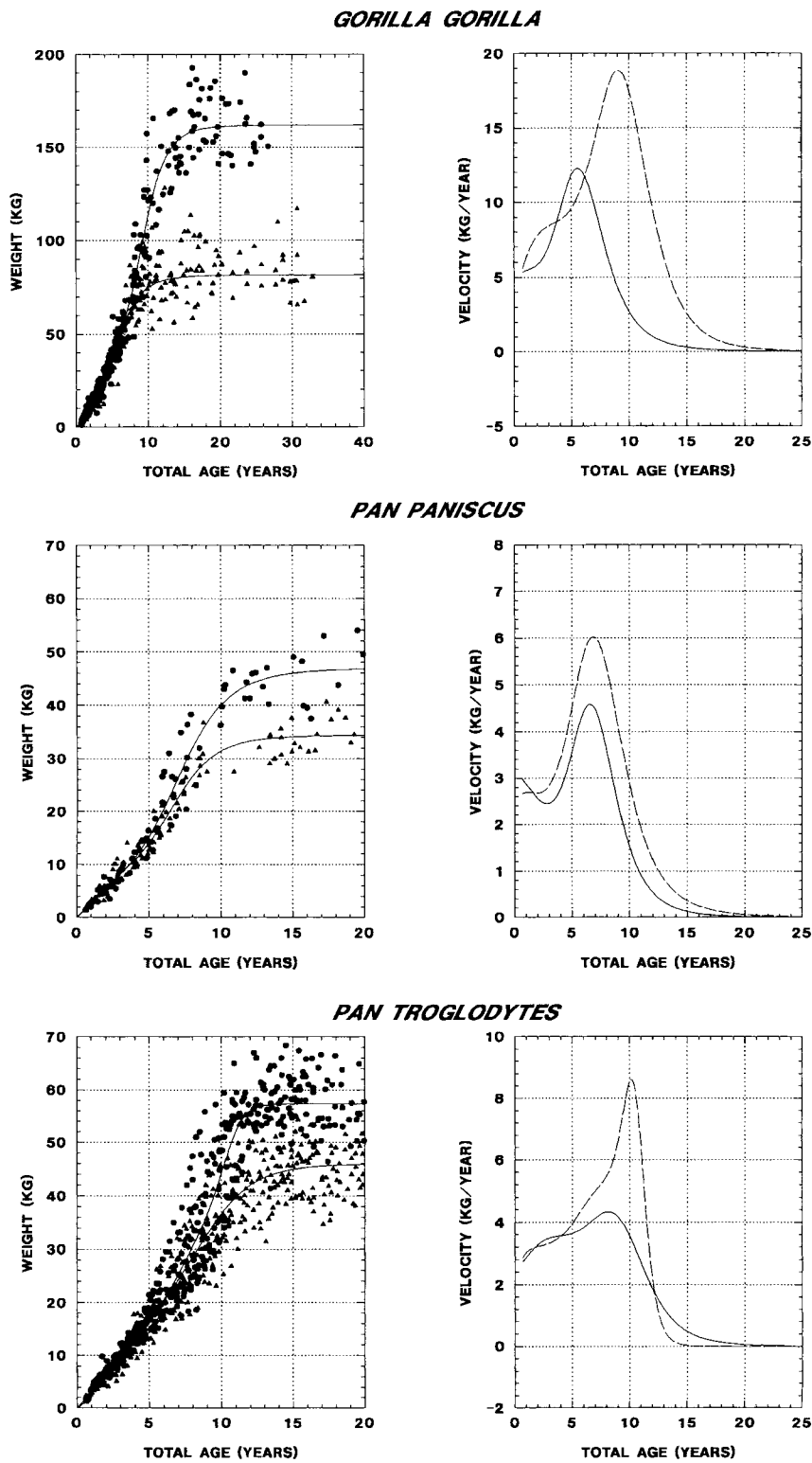


Fig. 10. Parametric models of growth data for African apes (JPPS model).

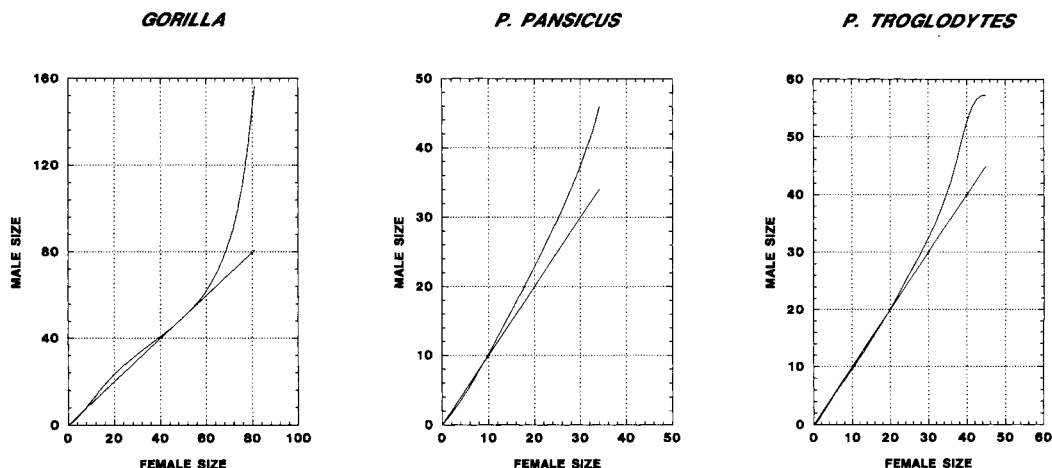


Fig. 11. Size trajectory curves by sex for each species.

1992). Variation in the control of growth is clearly shown by human studies that compare Ef  pygmies with other populations. Merimee et al. (1987) report that low levels of insulin-like-growth-factor I (IGF-I) in the Ef  are associated with decreased growth rates and depressed growth spurts despite levels of growth hormone (GH) that are comparable to individuals from other populations (see also Geffner et al., 1994). The Ef  also appear to be resistant to supplemental GH. Baumann et al.'s (1989) study complicates this problem by indicating that low levels of IGF-I in the Ef  are associated with decreased levels of growth hormone binding protein (GH-BP) receptors relative to other human groups. This result, coupled with resistance to growth hormone, suggests that the Ef  have reduced numbers of growth hormone receptors relative to other humans (Baumann et al., 1989).

Sex differences in the hormonal control of growth are suggested by Merimee et al. (1991). They report that male growth acceleration (pubertal growth spurt) is a consequence of the increased sensitivity of the GH-receptor-IGF-I system brought about by testosterone (or another unknown gonadal growth hormone). Other sources indicate that testosterone induces the growth spurt by increasing growth hormone production (Zachmann, 1992). For females, on the other hand, Merimee et al. (1991) suggest that

growth acceleration results from increased GH secretion. The magnitude of the female growth spurt appears to be independent of estrogen levels. The presence of ovarian estrogens, but not adrenal androgens, is required for normal female growth spurts (Zachmann, 1992). Thus, human studies show that the hormonal bases of growth spurts vary between sexes and among populations. We can speculate that similarly diverse mechanisms influence African ape growth, given that insights based on control of human skeletal growth can be applied to mass growth.

The present analysis provides information that is required for analyses of growth control in apes. Variability in growth rates, durations, and especially in the timing and magnitude of growth spurts in African apes described by the present study strongly implies that these species provide an excellent opportunity to gain significant and fundamental insight into the endocrine control of growth. In addition, the present study, in assembling data for over 200 individual animals, implies that endocrinological studies of these species in captivity (and possibly in the wild) are feasible.

Evolutionary processes. A second set of implications revealed by the present research centers on investigation of the evolutionary factors that have resulted in ontoge-

netic variability within and among these species. We have discussed factors that may be related to the evolution of ape sexual size dimorphism (Leigh and Shea, 1995), but have neither specified nor considered hypotheses to account for interspecific ontogenetic variation.

We suggest that much of the ontogenetic variation in apes can be understood with respect to Janson and van Schaik's (1993) model predicting negative correlations between growth rate and ecological risk. Specifically, this model anticipates evolution of low growth rates when high levels of ecological risk result from intraspecific feeding competition. Low growth rates minimize metabolic costs per unit time, and can evolve in primates because selection for rapid maturation via predation tends to be minimized by group living. However, Watts and Pusey (1993) identify problems in the application of this model to great apes for two major reasons. First, Watts and Pusey suggest that the kinds of intraspecific feeding competition discussed by Janson and van Schaik (1993) do not unambiguously characterize chimpanzees (presumably common chimpanzees). Second, they also argue that predation is not high enough in *Gorilla* to account for early maturation. We can note that growth rate data are required for tests of Janson and van Schaik's model because this model makes an explicit statement about the relation between growth rate and ecological risk. Although Watts and Pusey lack sufficient growth rate data, they reviewed the only available body weight growth literature (Shea, 1983) and present detailed information about the timing of maturational events. While some inferences about growth rates are possible with this information, data regarding the timing of growth events do not allow an adequate evaluation of Janson and van Schaik's model. Constant growth rates (linearity) may be implicitly assumed when growth durations and adult mass are used to estimate growth rates. As shown by the present analysis, growth rates vary in these species, and this variation may have significant implications with respect to Janson and van Schaik's model by implying that ecological risks modulate during ontogeny. It can be added that growth rates and

durations are not necessarily strongly correlated (Leigh, 1992a).

An additional difficulty with Watts and Pusey's (1993) suggestion is that differences in feeding competition (and therefore, ecological risk) among these species appear to covary predictably with growth rate variation. Comparisons of absolute and specific growth rates between *Gorilla* and *Pan* (especially common chimpanzees) seem to fit this model, in part because of an association between folivory and high growth rates in *Gorilla*. Janson and van Schaik explicitly predict high growth rates in folivores because leaves are typically ubiquitous and predictable: factors which should reduce ecological risks (1993). High growth rates have independently been suggested as one of several adaptations that differentiate folivores from nonfolivores (Leigh, 1994a), accompanying dental and gut specializations that facilitate consumption of high-fiber resources by folivores (Kay, 1984; Fleagle, 1988). Elevated growth rates may confer additional advantages to gorillas and other folivores, including metabolic advantages to early attainment of large size and early maturation of the alimentary system, especially if the gut scales with positive allometry during ontogeny (see Leigh, 1994a). Therefore, we suggest that high growth rates in gorillas are partly related to folivory through physiological advantages of rapid growth and reductions in ecological risks. Obviously, we cannot rule out the possibility that a derived size increase is related to increased folivory in gorillas.

Ecological risk in gorillas is further reduced relative to common chimpanzees because they utilize large and ubiquitously distributed food patches (Wrangham, 1986). Enhanced growth rates might also confer reproductive advantages to females because early maturation (or early attainment of an "optimal" female adult size) is not constrained by slow growth (Rubenstein, 1993; Pagel and Harvey, 1993). We must note that lowland gorillas (studied here) are likely less folivorous than mountain gorillas (Tutin and Fernandez, 1985, 1993), which serve as the basis for most of our information about *Gorilla* adaptations (Watts, 1984, 1985, 1990, 1994). However, levels of folivory in lowland

gorillas are probably sufficient to reflect adaptations that characterize other folivorous primates (over 40–45% of annual time spent feeding on folivorous resources seems to be sufficient to reflect this adaptation [Leigh, 1994a]). Thus, the present analysis suggests that Janson and van Schaik's (1993) model has predictive power for explaining why gorillas grow more rapidly than other African apes, and contributes to an understanding of adult size differences between genera.

Evaluations of the applicability of Janson and van Schaik's model to ontogenetic differences within *Pan* are complicated because contrasts between species are often subtle. However, our data seem consistent with this model, particularly with respect to female ontogeny. Our analysis shows that growth rates for males of each species are quite comparable, with differences in growth duration mainly accounting for the size variation between adult averages. Thus, factors that are associated with male size differences in *Pan* probably are most important late in ontogeny. It is difficult to precisely speculate what such factors might be because of insufficient (to our knowledge) behavioral studies that address the transition from the pre-adult to adult period, especially for pygmy chimpanzees. It is plausible, however, that a higher degree of arboreality in *Pan paniscus* may favor smaller size (Doran, 1993) that is achieved through truncating the duration of ontogeny relative to *Pan troglodytes*. Despite differences in adult locomotor behavior, the ecological risks encountered by males of each species are probably very similar. Socioecological information seems to suggest that levels of intermale aggression do not appear to differ greatly between species (Wrangham, 1986).

Female pygmy and common chimpanzees likely do encounter different risk profiles throughout ontogeny and as adults, leading to distinctive ontogenies. We suggest that female common chimpanzees face greater overall risks than pygmy chimpanzees because of relatively high levels of interfemale competition (White and Wrangham, 1988). Although female common chimpanzees do not form foraging groups (Watts and Pusey, 1993; White and Wrangham, 1988), clear interfemale competition in common chimpan-

zees has been related to foraging strategies that focus on frugivorous resources that occur in small, dispersed patches (White, 1989; White and Wrangham, 1988). This implies high levels of ecological risk, and would require modification of Janson and van Schaik's model to include species that encounter high ecological risks as a result of intraspecific feeding competition whether or not they form large groups. Competition for fruit resources that occur in relatively small and dispersed patches have virtually the same effect as competition within a large foraging group that utilizes large, evenly distributed patches.

Selection should favor large adult size for female *Pan troglodytes* as a result of feeding competition, conferring metabolic as well as direct competitive and antipredator advantages. However, the attainment of large size may be constrained by high ecological risks during ontogeny, resulting in depressed growth rates. One way to circumvent this constraint may be to extend the growth period, reaching large size and avoiding increased metabolic costs that would be incurred by supporting a growth spurt. Therefore, we hypothesize that a prolonged growth period has evolved in response to interfemale feeding competition in *Pan troglodytes*. This resource competition is directly analogous to sexual selection for prolonged growth in males that can evolve as a response to mate competition in some species (Jarman, 1983; Leigh, 1995; Wiley, 1974).

Pygmy chimpanzee females tend to be highly affiliative, an attribute that has been related to foraging for ubiquitously distributed resources that occur in large patch sizes (White, 1989; White and Wrangham, 1988). Elevated use of high fiber resources (Malenky and Wrangham, 1994) may help reduce feeding competition in *Pan paniscus* (Wrangham, 1986) and require high growth rates as an adaptation to such resources (Leigh, 1994a). Despite large group sizes in pygmy chimpanzees, we suggest that lower levels of feeding competition may be reflected by high peak velocities in pygmy chimpanzees relative to *Pan troglodytes*. Therefore, reduced feeding competition plus possible increases in utilization of folivorous resources may account for the presence of a

distinct growth spurt in female *Pan paniscus*, even though this species grows slower than common chimpanzees during the earliest phases of ontogeny. This pattern is interpretable within the framework of Janson and van Schaik's (1993) model if the pronounced growth spurt in *Pan paniscus* (especially females) reflects low levels of ecological risk, possibly only during a particular age range.

Competitive advantages to large size would not be expected for female *Pan paniscus*, in contrast to common chimpanzees. As for males, smaller size relative to common chimpanzees may be favored by selection for efficient arboreal locomotion (Doran, 1992, 1993), leading to smaller size relative to common chimpanzees. Despite strong similarities in the ontogeny of locomotor behavior between *Pan* species, adult locomotor behaviors are very distinct (Doran, 1992), possibly implying differences in selective pressures late in ontogeny.

Consideration of detailed ontogenetic data seems to suggest that Janson and van Schaik's (1993) model can be applied to apes. Growth rates appear to vary in directions that are predictable based on knowledge of variation in feeding competition for these species. While this analysis offers inferential support to this model, we must stress that direct measures of growth rate and ecological risk in free-ranging populations are required for further testing.

CONCLUSIONS

Analyses of mass growth in African apes show that the ontogenetic processes that lead to adult size in African apes vary (see Shea, 1983). The present analysis clarifies and extends Shea's previous analysis by more clearly defining the developmental processes that result in size differences within and among these species. Growth rate differences mainly account for differences in size between *Gorilla* and *Pan*. However, both rate and duration differences in growth account for size variation in *Pan* (common and pygmy chimpanzees), and the relative contribution of these differences varies by sex. Comparisons within *Pan* suggest that interspecific rate differences in growth are more

pronounced in females than in males. Sexual size dimorphism has variable bases in these species. Duration differences drive dimorphism in *Gorilla*, and are emphasized in *Pan paniscus*. Sex differences in the rate of growth almost exclusively result in dimorphism in *Pan troglodytes*.

This study documents substantial inter- and intraspecific variation in the timing and magnitude of "pubertal" growth spurts in African apes. Female common chimpanzees are unique in this group by not showing a clearly defined and unambiguous growth spurt. Analyses of absolute growth provide a foundation for endocrinological analyses of these species. The potential sex and population variation in human growth might imply that variation in ape growth control mechanisms is significant.

The variability in African ape size ontogeny can be interpreted within the context of a recent model that specifies a negative correlation between growth rate and ecological risk (Janson and van Schaik, 1993). An association between growth rates and ecological risks may be particularly important in influencing the evolution of growth in gorillas relative to *Pan*. Ecological risks seem to be high in female *Pan troglodytes*. Differences in risks faced by males between *Pan* species seem to be less obvious. These observations are consistent with predictions based on Janson and van Schaik's model.

ACKNOWLEDGMENTS

We thank Drs. Robert Anemone and Linda Winkler for inviting us to participate in their symposium. This research was aided by the dedicated curatorial and animal care staffs at the institutions from which data were obtained. We thank these individuals and institutions, including Dr. Anne Baker (Brookfield Zoo); Drs. Tom Meehan, Jim Letcher and Ms. Pat Sass (Lincoln Park Zoo); Dr. Andy Teare and Mr. Jan Rafert (Milwaukee County Zoo); Ms. Ingrid Portan (St. Louis Zoo), Dr. Amy Shima and Ms. Kay Munduate (San Diego Zoo and San Deigo Wild Animal Park); Dr. Doug Armstrong and Ms. Sarah Junior (Henry Doorly Zoo, Omaha); Dr. Tim Reichard (Toledo Zoo); Dr. Albert Lewandowski (Cleveland Zoo); Dr. Richard Cambre

(Denver Zoo); Dr. Mike Burton (Cheyenne Mountain Zoo, Colorado Springs, Colorado); Drs. Paul Calle, Danny Wharton, Fred Koontz, and Robert Cook (Bronx Zoo); Dr. Lynne Kramer (Columbus Zoo); Dr. Mark Campbell (Cincinnati Zoo); Dr. Julian Duvall (Indianapolis Zoo); Drs. Debra Forthman, Beth Stevens, and Rita Macmanamon and Ms. Cindy Thorstad (Atlanta Zoo); Dr. Roy Burns (Louisville Zoo); Dr. Mark Peckham, Dr. Joe Flanagan, and Ms. Barbara Lester (Houston Zoo); Ms. Donna Todd and Dr. Rodney Walker (Jackson Zoo); Drs. Mark Stetter and Susan Wells (Audubon Park Zoo, New Orleans); Mr. Jake Yelverton (Louisiana Purchase Gardens and Zoo, Monroe, LA); Ms. Linda Sanders (Baton Rouge Zoo); Mr. Will Sugg, Drs. Edwin Gould and Benjamin Beck (National Zoological Park); Drs. Ben Gonzales, Gary Kuehn and Mr. Victor Bolanos (Los Angeles Zoo); Dr. Les Shobert (North Carolina Zoo); Ms. Greta Macmillan (Knoxville Zoo); Mr. Donald Moore (Syracuse Zoo); Drs. Jim Else, Harold McClure, Jeremy Dahl and Ms. Sue Setzekorn (Yerkes Regional Primate Research Center, and grant number RR00165); Dr. Freeland Dunker, Ms. Gail Hedberg, and Dr. Myron Sulak (San Francisco Zoo); Mr. Robert Evans (San Antonio Zoo); Dr. James Kirkwood (London Zoo); Mr. F.M. Lockyear and Mr. Peter Halliday (Port Lympne and Howletts Zoo Parks); and Dr. Nate Flessness (International Species Information System). Dr. David Watts provided helpful comments and advice. Dr. Laurie Godfrey and two anonymous reviewers offered constructive comments during the review process. Financial support for this research was provided by Northwestern University, Sigma Xi, the Wenner-Gren Foundation, and the National Science Foundation grant number DBS9225084.

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